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Visual cues for attention following in rhesus monkeys

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Abstract

It is now well established that great apes follow human gaze direction. Despite physiological evidence showing cells in macaque temporal cortex sensitive to direction of eye gaze, there has been little evidence in non-ape species of similar abilities. The aim of this study was to investigate, at a behavioural level, whether monkeys can use static gaze, head, and body cues of conspecifics to interpret the direction of attention of others. We recorded the looking behaviour of 2 rhesus monkeys elicited by the presentation of photographs of conspecifics directing their attention in space. With photos of monkey stimuli whose head and body were oriented in different or similar directions, we found that the head but not the body was used by the monkey subjects to orient their own attention. With photos of monkey faces oriented to the camera while gaze was averted left, right, up or down, we demonstrated that monkeys are able to spontaneously follow gaze of conspecifics. With photos of monkey heads oriented 45 degrees to the right or left, attention following was stronger when the gaze direction was consistent with

the head orientation than when the eyes were directed towards the observer. Our studies show that both head orientation and eye gaze influence the observer's orienting responses.

Key words: Gaze following, attention direction, looking behaviour, facial cues, rhesus monkeys.

INTRODUCTION

One of the primary cognitive mechanisms enabling human social interaction and communication is the ability to follow the attention direction of others (Baron-Cohen, 1994). For instance, to understand where, and hence at what, an individual is looking, visual cues such as gaze direction, head position and/or body posture can be used to orient the observer's attention towards the same place of interest in the environment. There is increasing behavioural and physiological evidence suggesting that this ability to follow attention is present in non-human species, including great apes (e.g., Povinelli & Eddy, 1996a; Itakura & Tanaka, 1998), monkeys (Emery, Lorincz, Perrett, Oram, & Baker, 1997; Tomasello, Call, & Hare, 1998) and dogs (Miklósi, Polgárdi, Topál, & Csányi, 1998). The nature and relative importance of the visual cues supporting this ability, however, remain confused. Some authors do not discriminate between the cues available to subjects (eyes, head, or body posture) and the different conjunctions of these cues. In natural situations the evidence available from different cues may not be congruent. For example, the head may be oriented in one direction but the eye gaze may be in a different direction.

The terms attention following, gaze following, and joint attention have often been used interchangeably but may be considered different yet related abilities (Emery et al., 1997). Here, attention following will be considered as the general ability of one individual to follow the direction of attention given by any body cue (e.g. gaze, head, or body posture) from a second individual to a position in space. In this study, gaze refers more specifically to eye gaze, i.e., the orientation of the eyes. Joint attention requires the additional process of combining the attention of both individuals onto a common object or focus of attention and can be considered a triadic interaction (Emery et al., 1997).

Human infants begin to follow attention as early as 3-4 months of age as long as the direction of attention is specified by at least the head direction of the adult (Scaife & Bruner, 1975; Vecera & Johnson, 1995; D'Entremont, Hains, & Muir, 1997). More complex attention following responses emerge in older infants (6-18 months) with the use of the eyes to locate accurately the focus of another's attention (Butterworth & Jarrett, 1991; Moore & Corkum, 1998). By two years of age, children begin to be able to use eye gaze direction to infer desires of others (Lee, Eskritt, Symons, & Muir, 1998). Finally, by the age of 4 years, they can accurately follow gaze when eye cues are presented in an impoverished context such as drawing (Baron-Cohen, 1994).

In non-human primates, visual signals including gaze may play a central role in social interaction. They can provide information about emotional state (e.g., threat includes eye contact, submission includes gaze aversion), the direction of attention (Chance, 1962; Perrett & Mistlin, 1990; Emery et al., 1997) and the intention of actions (Jellema, Baker, Wicker, & Perrett, 1999). Monitoring cues to the direction of attention may allow an individual to gain information about the location of food and predators, social dominance and mating behaviour (Menzel & Halperin, 1975; van Schaik, van Noordwijk, Warsono, & Surtiono, 1983). Attentional cues containing directional information like gaze, head and body posture could be the foundation of referential communication and participate in the process of vicarious learning (Mineka, Davidson, Cook, & Keir, 1984; Emery & Perrett, 1999; Perrett, 1999).

There is evidence that great apes have the ability to use such a referential aspect of focus of attention. For instance, in a problem solving experiment where a gorilla needed to request help from a human experimenter in order to reach a goal, the gorilla alternately looked between the goal (object of attention) and the eyes of the experimenter (Gómez, 1990). In the same fashion, attention following abilities seem to be used as a subterfuge to create false belief in conspecifics, for instance to gain food "safety", in what has been called "tactical deception" (Whiten & Byrne, 1988). For example, an individual will look in the opposite direction of the food he/she covets, to attract the attention of a second individual away from the food. Humans and great apes may share cognitive mechanisms through which gaze following and shared attention act as precursors to the development of theory of mind (Baron-Cohen, 1994). Alternatively, gaze following may more simply be a quasi-orienting-reflex that allows a social individual to orient to important

events (Povinelli & Eddy, 1996; Moore & Corkum, 1994; Friesen & Kingstone, 1998; Langton & Bruce, 1999).

Chimpanzees and orang-outans will follow the direction of attention of humans (Povinelli & Eddy, 1994, 1996a, 1996b, 1997; Itakura, 1996; Itakura & Tanaka, 1998) and conspecifics (Tomasello et al., 1998). Cues manipulated include orientation of the head and eyes and the use of gestures (e.g., pointing). In the majority of studies, movement is involved in the attentional cues (e.g., head and eyes turning in a particular direction) and multiple cues are presented. For example, Povinelli and Eddy (1994, 1996a, 1996b) found that young chimpanzees will follow the attention direction of humans when specified by movement of the head and eyes or movement of the eyes alone. Similarly, Itakura and Tanaka (1998) found that chimpanzees and an orang-outan were able to use experimenter-given cues in an object-choice task, including tapping, gazing (head and eyes), pointing, gazing alone, and glancing (eyes alone). At the start of each trial the experimenter was looking at the mid-point between the two objects and therefore all cues also included a movement component. The ability to follow attention is seen in chimpanzees even when the focus of attention of the experimenter is located behind the subject or beyond an opaque object (Povinelli & Eddy, 1996a, 1997).

In monkeys, there is conflicting evidence for attention following. In object-choice tasks, capuchin and macaque monkeys failed to use conjoint head and gaze orientation of a human experimenter to guide their responses although they could learn to use gestural cues such as pointing (Anderson, Sallaberry, & Barbier, 1995; Anderson, Montant, & Schmitt, 1996). One capuchin, however, after 120 trials with sequential introduction of different cues, learned to use combined head and gaze orientation (Itakura & Anderson, 1996). Itakura (1996) reported that non-ape species (including macaques and capuchins) failed to follow attention direction specified by conjoint movement and orientation of the head and eyes.

In all of these studies in monkeys, the stimulus for attention following was the experimenter. In experiments with a conspecific as the stimulus, attention following has been observed (Emery et al., 1997; Tomasello et al., 1998). For example, Emery et al. (1997) analysed the spontaneous behaviour (looking behaviour) of 2 rhesus macaques during the presentation of a video-film of conspecifics directing their attention towards one of two identical objects. Cues specifying the direction of

attention included orientation of the head and body with some movement. Both monkey subjects inspected the target location (object or position attended by the stimulus monkey) more than the distracter (non-attended object or position). Tomasello et al. (1998) showed that four species of monkeys (rhesus, pigtail and stump-tail macaques, and sooty mangabeys) followed the attention direction of conspecifics onto a distal object (although pigtail macaques failed to show evidence of attention following with more stringent criteria). Cues specifying the direction of attention in this experiment included orientation of the head and eyes of the stimulus monkey and any associated movement.

The studies of attention following described in monkeys have manipulated many different visual cues to attention direction (i.e., body posture, head, gaze, and any associated motion). It is not clear whether monkeys can make use of eye gaze signals alone to determine the direction of attention in extra-personal space.

There is clear evidence showing that monkeys process gaze signals directly addressed to them. Indeed monkeys as young as 3 months of age exhibit a variety of expressions (appeasement, fear, etc.) to faces depending on whether the stimulus face makes eye contact or not (Redican, Kelliecutt, & Mitchell, 1971; Keating & Keating, 1982; Mendelson, Haith, & Goldman-Rakic, 1982; Perrett & Mistlin, 1990). Such studies show that monkeys react to gaze signals of an agent when the agent directly looks at the observer (that is, when the agent's attention was directed at the observer itself).

At the neurophysiological level there is evidence for the coding of attention direction, even when specified by eye gaze alone. Cells responsive to face stimuli in the temporal cortex and amygdala of macaque, have been found that are sensitive to the eye region and to gaze direction (Leonard, Rolls, Wilson, & Baylis, 1985; Perrett, Smith, Potter, Mistlin, Head, Milner, & Jeeves, 1985; Perrett, Harries, Mistlin, Hietanen, Benson, Bevan, Thomas, Ortega, Oram, & Brierty, 1990; Perrett et al., 1993; Perrett & Mistlin, 1990; Brothers & Ring, 1993). In particular, in the superior temporal sulcus, cells are found responsive to particular face and body orientation and views (Wachsmuth, Oram, & Perrett, 1994; Perrett et al., 1985). Rather than coding the geometric features of different facial views, some of these cells code the attention direction. These cells show response generalisation across different views, orientations, and postures of the body and head as long as the available cues suggest that attention is maintained in a given direc-

tion (Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1985, 1990, 1993; Walsh & Perrett, 1994). Particular populations of cells code for attention directed towards the observer, other populations code for attention directed to locations in extra-personal space (e.g., up, left, or right). For these cell populations, visual information from different origins (body, head, and gaze) is combined in a compatible manner. If a cell responds to gaze left, the same cell may respond to the left profile view of the face when the eyes are not visible, or to the left profile view of the body if the head is occluded from sight (Perrett et al., 1985; Wachsmuth et al., 1994). In combining the cues, for some cells the eye direction takes priority over the head direction and the head direction over the body direction (Perrett et al., 1985, 1990, 1992; Jellema et al., 1999). In other cases the information from the eyes, face, or body make independent contributions, with no particular priority. These physiological results indicate extensive neural processing of cues to the attention direction of others. Within these cues it would appear that eye gaze cues have a powerful role, so it is surprising that there is no behavioural evidence for pure gaze processing in monkeys.

In the present study we investigated the spontaneous reactions of macaques (in terms of looking behaviour) to static images of conspecifics directing their attention in space. The pattern of eye movements and duration of fixations on static images have been widely used as measures of preference and perceptual development (Humphrey, 1974; Keating & Keating, 1982; Mendelson et al., 1982; Wilson & Goldman-Rakic, 1994; Emery et al., 1997). Such studies show that monkeys respond to photographic images of social stimuli in a manner similar to natural real stimuli (e.g., Perrett & Mistlin, 1990). Monkeys discriminate between images of human, monkey, and schematic faces from non-face stimuli (Keating & Keating, 1982) and differentiate between pictures of different animal species and between individuals of the same species (Humphrey, 1974; Rosenfeld & Van Hoesen, 1979; Dittich, 1994). Furthermore, monkeys respond differentially to images of facial expressions with species typical emotional responses such as vocalisation and lip smacking (Redican et al., 1971; Sackett, 1966; Mendelson et al., 1982; Perrett & Mistlin, 1990).

The current study assesses the relative importance of different visual cues to attention direction. The three cues for attention direction manipulated were orientation of the head, body posture, and eye gaze. Since static images were used, movement was not available as a cue for the

direction of attention. The first experiment investigated the relative importance of head and body orientation. In some cases the head and body orientation of the stimulus monkey were in the same direction (compatible cues), whereas in other stimuli head and body orientation were in different directions (incompatible cues). We predicted that subjects would follow the attention direction given by the orientation of the head when there was a conflict between the orientation of the head and body. The second experiment investigated the ability to follow eye gaze alone. The stimuli consisted of static, frontal view of macaque heads with the eyes orientated in different directions (up, down, left, or right). We predicted that subjects would follow the gaze direction and look more frequently in the direction given by the gaze than in the other directions. The final experiment investigated the interaction between head orientation and gaze direction. The stimuli showed macaque heads oriented 45 degrees to the right or left with the eyes either directed in the same direction or at the observer. We predicted that the subjects would be more likely to follow attention when the head and gaze direction were consistent.

METHOD

Subjects

The subjects were two male rhesus macaques (Terry and Steve, 4 and 6 years old, respectively) born and reared in a social colony of conspecifics. During the experimental period the subjects were housed individually but in visual and auditory contact with other macaques. The subjects had previously seen slides as well as video-film of humans, conspecific monkeys and other animals and had participated in an earlier study on gaze following (Emery et al., 1997). Both subjects were also involved in concurrent electrophysiological studies. All experiments were performed under appropriate UK Home Office Licenses and were regulated by the University of St Andrews Animal code of Practice.

Set-up and testing

The subject faced a rectangular white screen (222 by 183 cm) situated 450 cm away onto which stimuli were projected in a darkened room

using a slide projector (Kodak Ektapro 5000). The screen contained 5 embedded LEDs used for calibration of the eye position. The LEDs were located at the screen centre and at the middle of each edge of the screen.

The looking behaviour of the subject was recorded with an infrared camera mounted inside a box attached to the front of the primate chair (see for details Hietanen & Perrett, 1993). The stimuli were viewed through a liquid crystal shutter (Screen Print Technology - rise time <15ms) under computer control. A further camera mounted above the head of the subject recorded the test stimuli projected on the screen. A time and frame code was added to the image from the first camera (VITC time-code generator and frame counter - Horia VG50) and the output sent to 2 separate video recorders. A video record of eye position and a time code were recorded on one recorder (Akai VHS VS - 603EK). A record of the eyes and the time code was mixed (Panasonic VHS video mixer, WJAVE7) with the record of the test stimuli and recorded on a second recorder (Panasonic NV - FS200B).

Before each testing procedure, the eye movements were calibrated. The monkeys had been previously trained to perform a colour discrimination task dependent on the colour of an LED. Licks during the presentation of a green LED were rewarded with fruit juice whereas licks during the presentation of a red LED were discouraged with no reward or a mildly aversive saline solution. A 500 ms tone was sounded before the illumination of the LED, lasting 3 s. The colour of the LED was varied in a pseudo-random order under computer control. For calibration, the LED at each position was presented at least twice. Then, the LEDs were turned off and the tone was presented on its own to habituate any behavioural tendency to search for LED lights on the screen.

Test stimuli and procedure

The stimuli were colour slides of monkeys taken with a Nikon camera (F-801). The monkeys were attracted to look intently in one direction (left, right, up, down, or at the camera) by presenting interesting stimuli (e.g., hand puppets or fruit) at the desired location.

Experiment 1: Head and body cues. Photographs of individual monkeys were taken through a glass window in a colony room. The mon-

keys in the photographs were looking either to the right or to the left. Orientation of the head and body varied across the photographs. In some photographs, the head and body were oriented in the same direction (e.g., body left, head left; Figure 1a), whereas in others the head and body were oriented in different directions (e.g., body left, head right; Figure 1b). Eye gaze direction was always compatible with head direction. The photographs were digitised with a flatbed scanner (Epson GT-6500) and the background cropped to leave a centrally positioned stimulus monkey. The stimulus slides were made out of these pictures (resolution, 1900 by 1400 pixels at 24-bit colour).

The image of the monkey stimulus was displayed at the same height as the subject. The size of the head and body stimuli ranged from 6.4 to 10.2 degrees of visual angle.

The stimuli were presented on 20 trials (10 compatible head and body cues, 10 incompatible head and body cues), each of 3 s duration, and an inter-trial period of approximately 10 s. The trials were blocked into 5 sessions. Each session included 2 randomly selected compatible and 2 incompatible head and body slides interspersed with trials with non-test slides. The sessions were run at intervals of 2-3 days and were preceded by calibration trials. Presenting few stimuli on a given day was designed to avoid habituation.

Experiment 2: Gaze direction cues. Photographs were taken of the two monkey subjects seated in a primate chair. Black material was used to restrict the camera view to the head only. Photographs were taken of a frontal face view of the head with the eyes directed in the four cardinal directions (up, down, left, and right; Figure 2). The size of the head stimuli ranged from 6.7 to 7 degrees of visual angle.

Experiment 2 included 12 trials per condition, each trial of 5 s duration, and 10 s inter-trial intervals. The trials were blocked into 3 sessions containing one trial of each the 4 eye directions.

Experiment 3: Head and gaze direction cues. Photographs were taken of the head rotated 45 degrees away from the camera to give left and right half-profile views. In the "Head = Gaze" condition, the gaze was compatible with the head (e.g., head and eyes looking left, Figure 3a) and in the "Head \neq Gaze" condition, the gaze was directed at the camera (i.e., eye contact, Figure 3b). The size of the head stimuli ranged from 9.8 to 11.3 degrees of visual angle.

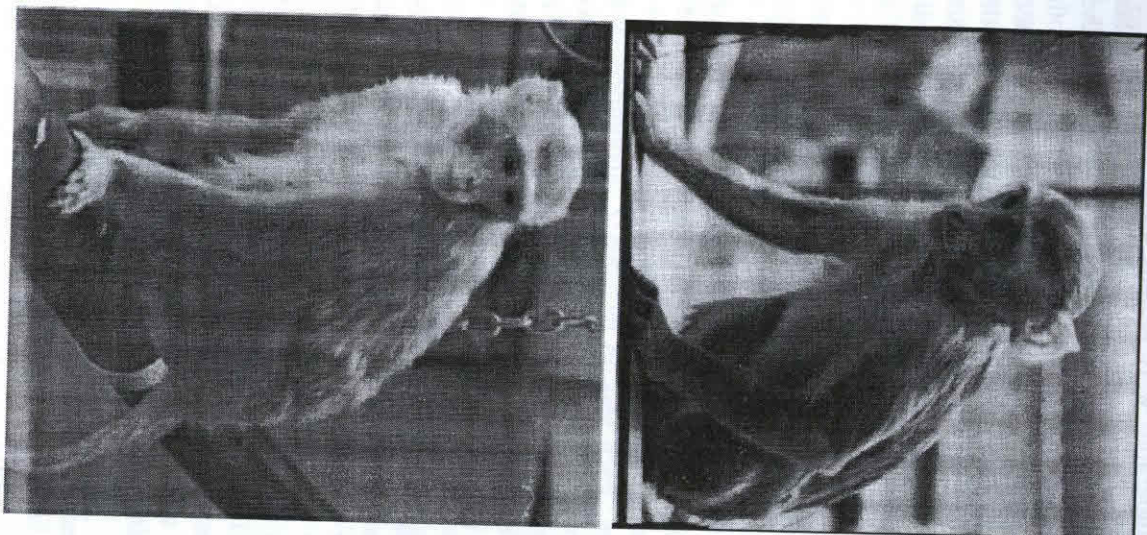


Figure 1. Examples of the head and body stimuli used in Experiment 1. (a) head and body oriented in the same direction, i.e., left; (b) head and body oriented in different directions, i.e., body left, head right.

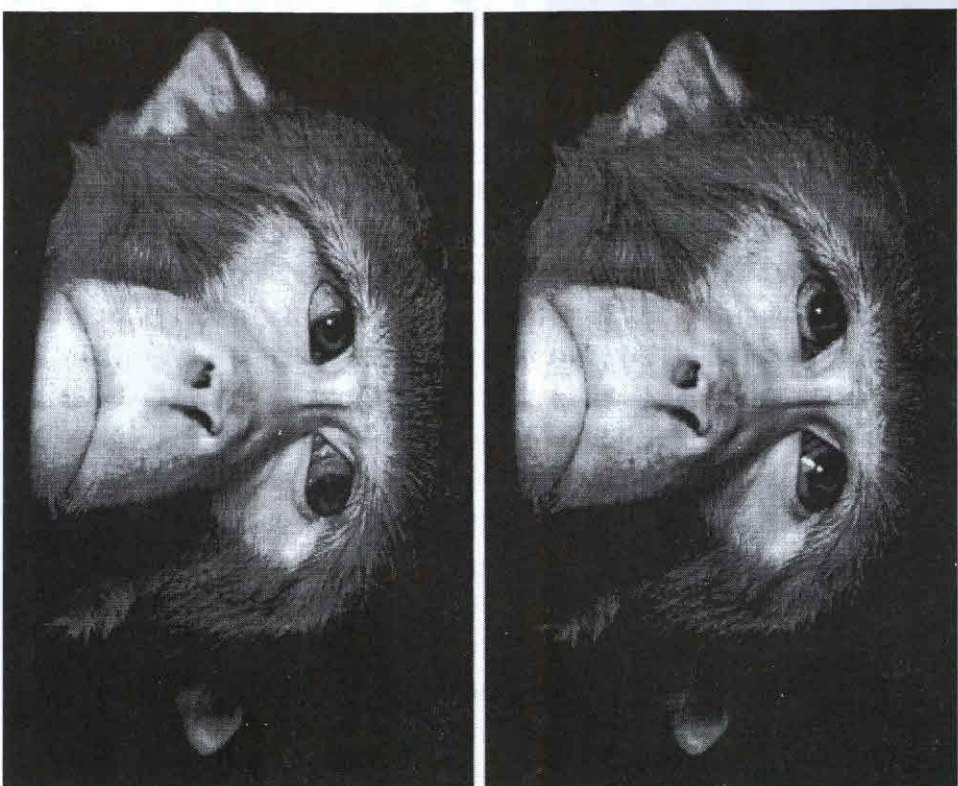


Figure 2. Examples of the gaze stimuli used in Experiment 2. Photographs of frontal face view of one of the monkey subjects with eyes directed up (a) and right (b).

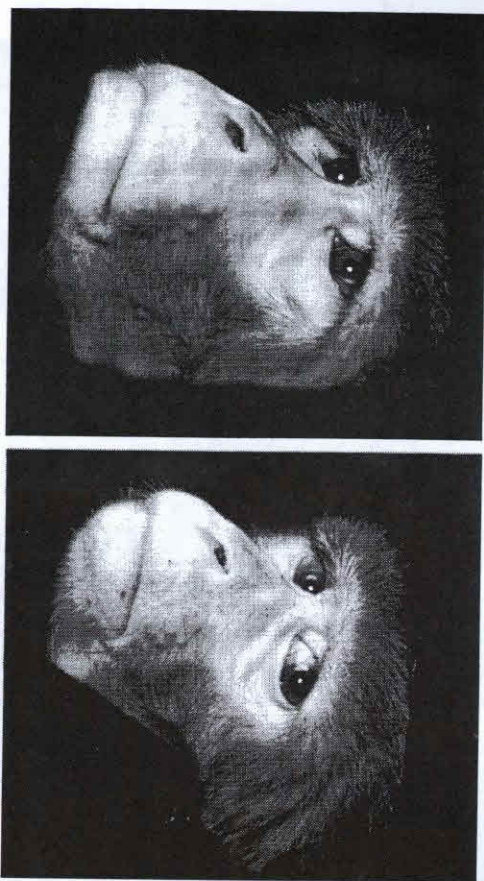


Figure 3. Examples of head and gaze stimuli used in Experiment 3. (a) "Head = Gaze" condition, head and gaze direction are compatible and oriented left. (b) "Head \neq Gaze" condition, head and gaze direction are incompatible; the head is directed left while the gaze is directed to the camera or observer.

Experiment 3 included 12 trials per condition, each trial of 5 s duration with 10 s inter-trial intervals. Experiment 3 was split up into 6 sessions of 4 trials equally mixing the two conditions ("Head = Gaze" and "Head \neq Gaze").

Evaluation of performance

The video of the subject's eyes only (including time code) was shown on a monitor with a distance between the centre of the pupils of 40 cm. The duration and position of fixations made by the subjects were recorded. Fixations are defined as a glance to one position of the screen with the eyes remaining static for at least 2 frames (80 ms). Inspections are defined as the sum of fixations of one area of the screen without intervening fixations of other areas. The duration of each inspection was defined as the cumulative number of video frames the subject spent at one area.

For Experiments 1 and 3, the screen was divided into 4 exclusive areas (following Emery et al., 1997). In these experiments the stimulus monkey was depicted directing attention in one of two peripheral directions (left and right). The target area (T) was defined as the position to which the head of the stimulus monkey pointed. A distracter area (D) was defined as an area of equivalent size in a position laterally opposite the target area. The area around the stimulus monkey was denoted (M) and all other areas on the screen and beyond were defined as elsewhere (E) (Figures 4a and 4c).

For Experiment 2, the screen was divided into five areas: 4 peripheral quadrants of equal area (up, down, right, and left) and a central area occupied by the stimulus monkey (M). In this experiment the stimulus monkey was depicted directing attention in one of these 4 quadrants. The quadrant attended by the stimulus-monkey is referred to as the target area (T), the opposite quadrant as the anti-target area (AT) and the 2 remaining quadrants as clockwise (C) and anti-clockwise (AC) to the target area (Figure 4b).

The analysis of the eye position consisted of attributing a judgement of which of these areas the subject was looking for each fixation. During the initial "blind analysis", attributions were simply made to areas labelled left, right, M, and E for Experiments 1 and 3, and quadrants labelled left, right, up and down, or M, for Experiment 2. Subsequently the areas and quadrants were re-coded.

From the score sheet, the mean number of inspections and fixations made on each of the four or five positions (depending of the experiment) as well as the duration of the inspections (calculated from the frame count) were calculated for each condition in the three experiments.

Data analysis

Previous studies have used either the duration of looking, or the position of looking. Our methods allow quantification of both the duration of inspection and the spatial distribution of inspection (Emery et al., 1997). Since these measures can yield different results we present an analysis of both measures.

The data from both subjects were analysed for the number of inspections and for the duration of inspections using a multi-factorial ANOVA. As the data on the number of inspections and duration of in-

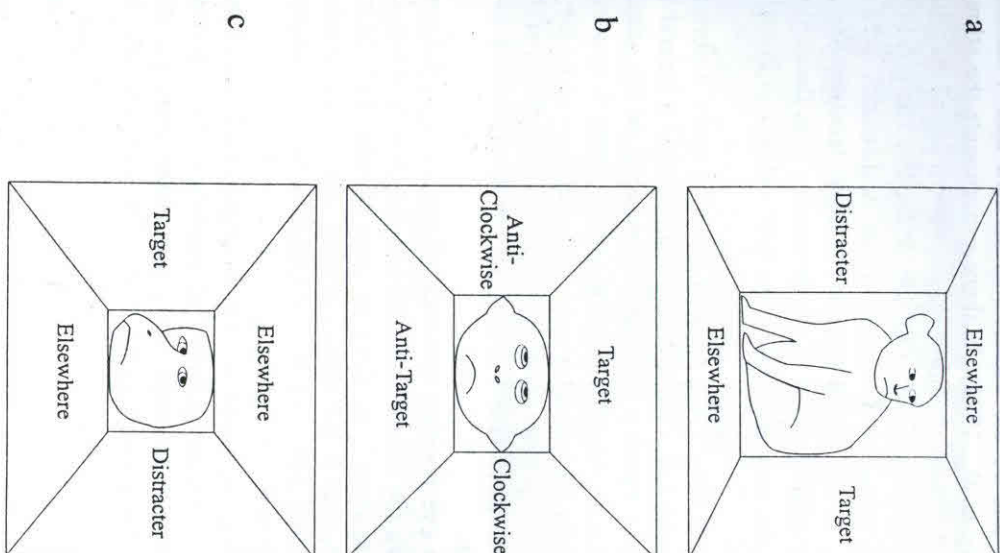


Figure 4. Areas delimited in judgements of subject's fixations. (a) Experiment 1: "Head right and body left"; (b) Experiment 2: "Eyes up"; (c) Experiment 3: "Head \neq Gaze".

A stimulus monkey attending to a target area occupied the central position of the screen. In experiments 1 and 3 (a and c), the target quadrant located either left or right of the stimulus monkey was given by the head direction, its mirror position determined the distracter area and the remaining areas were defined as elsewhere. In experiment 2, the quadrant opposite the target was labelled as anti-target, and the two remaining quadrants were labelled clockwise and anti-clockwise to the target area (b).

specions were not distributed normally but followed roughly a Poisson distribution, they were transformed using $\sqrt{(x+1)}$ before undergoing the ANOVAs. Post-hoc testing was performed using the Fisher's Protected Least-Significant Difference test (PLSD, Snedecor & Cochran, 1980).

For Experiment 1, a three-way ANOVA was performed on the total number of trials, with subjects, compatibility (head and body compatible/incompatible) and eye position (T, D, M, and E) as main factors. Experiment 3 was analysed similarly with a three-way ANOVA of the total number of trials, with subjects, eye/head compatibility, and position as factors.

For Experiment 2, a two-way ANOVA was carried out on the duration of inspection at a given position on each trial. The factors were subjects and position (M, T, AT, C, and AC). Another two-way ANOVA with subjects and quadrants as factors was dedicated to check that the subjects watched equally each quadrant. It was carried out on the total time spent in each quadrant (up, down, right, and left) regardless of their status (T, AT, C, and AC).

For each experiment, the frequency of inspections of the target position was compared to that expected by chance using the Binomial test. For Experiments 1 and 3, the number of inspections made of the target and distracter positions was compared to an expected probability of 0.5 (i.e., 50% of inspections should be made of the target position and 50% of the distracter position if inspection was random). For Experiment 2, the number of inspections of the Target quadrant (T) divided by the total number of inspections made of all 4 peripheral quadrants (T, AT, AC, and C) was compared to an expected probability of 0.25. After inspections of the central monkey stimulus have been excluded, one expects 25% of the remaining inspections to be in each of the 4 peripheral quadrants if inspections were made at random.

Analysis was made of the "first" fixation made of either the T or D positions for Experiments 1 and 3 (and of T, AT, C, or AC for Experiment 2) after the monkey subject had looked at the stimulus monkey. For each subject, this analysis compared the proportion of trials where the "first" fixation was made on T position against the expected probability (Experiments 1 and 3, $p = 0.5$; Experiment 2, $p = 0.25$). In Experiments 1 and 3, if the monkey subject did not look during a trial at either the target or the distracter position after watching the stimulus monkey (e.g., looking only at the monkey and/or the elsewhere positions), the trial was discounted from the analysis of "first" fixation.

A single scorer, "blind" to the stimulus conditions, performed the analysis. The inter-observer reliability was assessed with a second scorer (also "blind" to the stimulus conditions) independently analysing eye position from the video records of 12 trials in Experiment 2. The 2 scorers exhibited significant agreement (Cohen's kappa statistic $K = 0.564$, $p < 0.001$) on their ratings of the sequence of 132 fixations assigned to the 5 positions (left, right, up, down, and stimulus monkey).

EXPERIMENT 1: HEAD AND BODY CUES

Results

The sequence of inspections produced at the appearance of the slide always began by a fixation of the monkey or the elsewhere positions, with fixation of the monkey being more likely to occur (respectively for monkey and elsewhere positions: Terry: 13 M/7 E; Steve: 11 M/9 E). Fixations of the monkey were always of longer duration than fixations elsewhere (mean number of frames; Terry: 24.4 M, 2.9 E; Steve: 26.8 M, 3.4 E). Fixations in the elsewhere positions were always followed by a fixation of the monkey position. For most trials, the "first" fixation of the target or distracter positions immediately followed the initial fixation of the monkey (Terry: 15/18; Steve: 17/17).

Both subjects made a greater number of inspections of the target position than of the distracter position (Figure 5). The number of inspections made of the target position expressed as a fraction of the total number of inspections made of target or distracter positions across all trials was 17/22 for Terry (Binomial test, $p < 0.009$) and 28/39 for Steve ($p < 0.005$). Analysis of the "first" fixation on target or distracter or also showed that both subjects were more likely to look first at the target than distracter position (Terry: 14/18, $p < 0.015$; Steve: 14/17, $p < 0.006$).

The three-way ANOVA with subject, compatibility, and position as main factors showed a significant main effect of position on the number of inspections made, $F(3, 3) = 35.5$, $p = 0.008$, which relates, among other things, to a significantly greater number of inspections of the target than of the distracter ($p < 0.05$). Although for both monkeys there was a greater difference for the inspections made to the target compared to those made to the distracter in the incompatible body and

Head and body cues

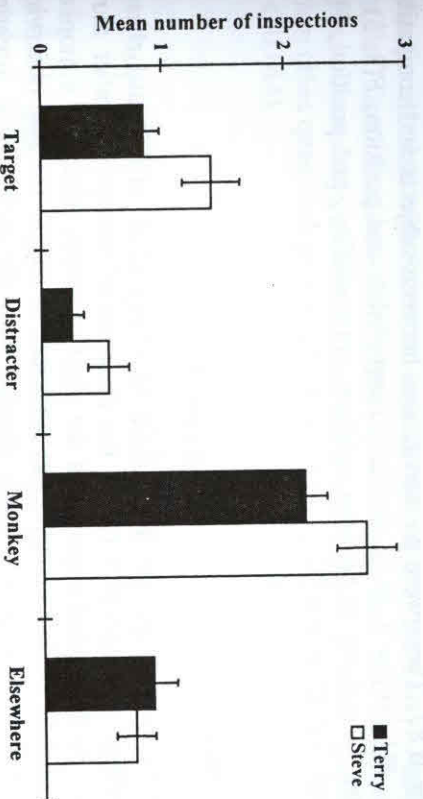


Figure 5. Number of inspections for head and body stimuli. Mean number of inspections (+/- SEM) made per trial of each stimulus position (target, distracter, monkey, and elsewhere). Each bar gives the average across 20 trials for Terry (grey) or Steve (white).

head cue condition than in the compatible body and head cue condition, this variation was not significant as reflected by a non-significant interaction between compatibility and position, $F(3, 3) = 2.04$, $p = 0.29$. There was no significant main effect of compatibility, $F(1, 1) = 0.01$, $p = 1.00$, or subjects, $F(1, 36) = 2.91$, $p = 0.10$, and no interactions between the main effects (subjects and compatibility: $F(1, 36) = 3.16$, $p = 0.08$; subjects and position: $F(3, 108) = 1.56$, $p = 0.20$; subjects, compatibility, and position: $F(3, 108) = 1.82$, $p = 0.15$).

The average duration of inspections (total number of frames) of each position per trial was analysed using a three-way ANOVA. There was a significant main effect of position, $F(3, 3) = 30.99$, $p = 0.009$. Post-hoc tests showed that this was due to a longer time spent looking at the monkey's position over the other positions ($p < 0.05$ each comparison) and that the average time spent looking at the target was not significantly greater than that for the distracter ($p > 0.05$). Of less importance, there was a significant interaction between subjects and position, $F(3, 108) = 2.80$, $p < 0.05$, the "Elsewhere" position being looked at

for longer by Terry than by Steve. There was no significant main effect of subjects, $F(1, 36) = 0.67$, $p = 0.42$; compatibility, $F(1, 1) = 0.05$, $p = 0.87$. There were no interactions between subjects and compatibility, $F(1, 36) = 1.19$, $p = 0.28$, compatibility and position, $F(3, 3) = 0.99$, $p = 0.50$, or between subjects, compatibility, and position, $F(3, 108) = 1.17$, $p = 0.32$.

Discussion

The results replicate the finding of Emery et al. (1997) that rhesus monkeys spontaneously follow the direction of attention of other monkeys. In the present experiment the sight of a static image of a monkey oriented to the left or right was sufficient to trigger the two observing subjects to look at a position aligned with the direction of attention demonstrated by the stimulus monkey. This result was evident for the analysis of the number of inspections and the position of initial fixations. Throughout these analyses, compatibility had no effect on the pattern of inspection: the subjects inspected a position indicated by the orientation of the head of the monkey stimuli. The alignment of the body in the stimuli made no impact on the pattern of fixation. Thus the subjects followed the head direction of the stimulus monkey and ignored the body direction.

Although this experiment failed to find evidence that body posture influences attention following in macaque monkeys, this does not mean that the body is uninformative about attention direction. Physiological evidence indicates that body posture may provide information about direction of attention (see Perrett et al., 1992) or the intentionality of an action (Jellema et al., 1999).

EXPERIMENT 2: GAZE CUES

Results

Both monkeys made more inspections of the target quadrant than of any of three remaining quadrants (Figure 6). The fraction of inspections of the target quadrant out of inspections of all 4 quadrants was greater than expected by chance ($p = 0.25$; Terry: 21/54, $p < 0.017$; Steve:

22/48, $p < 0.0014$). The sequence of inspections produced at the appearance of the slide always began by a fixation on the monkey's position for all trials with Steve, and on all but one trial for Terry. Analysis of the "first" fixations of peripheral quadrants on each trial also showed that both monkeys initially looked at the target quadrant more frequently than other quadrants ($p = 0.25$; Terry: 8/12, $p < 0.003$; Steve: 7/12, $p < 0.014$).

Gaze cues

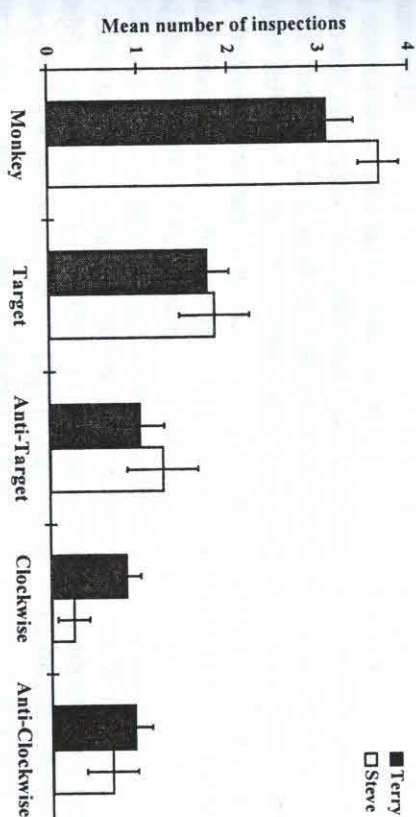


Figure 6. Number of inspections for eye gaze stimuli. Mean number of inspections (\pm SEM) made per trial of each stimulus position (monkey, target, anti-target, clockwise, and anti-clockwise). Each bar represents the average across 12 trials for Terry (grey) or Steve (white).

The analysis of the duration of inspection confirms this result. A two-way ANOVA (subjects and position of gaze as main factors) reported a significant main effect of positions, $F(4, 4) = 11.2$, $p < 0.02$, which reflected in part a greater time spent in inspecting the target quadrant than on any of the three other quadrants ($p < 0.05$). Each of the remaining quadrants (AT, C, and AC) was watched for an equal duration ($p > 0.05$). Of less interest, there was a significant main effect of subjects, $F(1, 22) = 4.36$, $p = 0.049$. The interaction between subjects and position was not significant, $F(4, 88) = 1.67$, $p = 0.16$ which confirmed that both monkeys followed the same observational pattern.

A second two-way ANOVA with subjects and quadrants as main factors was performed which showed that there was no existing bias in duration spent within any particular direction as there was no significant main effect of quadrants, $F(3, 3) = 3.11$, $p = 0.19$, and no subject and quadrant interaction, $F(3, 66) = 1.09$, $p = 0.36$. There was a significant main effect of subjects, $F(1, 22) = 5.30$, $p = 0.03$.

Discussion

Previous studies of attention following have rarely differentiated between head and gaze cues. To date, there is in fact no evidence for attention following in monkeys using cues derived solely from the orientation of the eyes. With natural (conspecific) stimuli it becomes almost impossible to control gaze and head cues independently. With human experimenters acting as stimuli, gaze direction is easier to control, yet monkeys fail to use human gaze as a visual cue in discrimination learning experiments. The use of static photographs allows the role of gaze cues from conspecifics to be assessed unambiguously. The results of Experiment 2 are clear and by each of the measures used (number of inspections, duration of inspection, and "first" fixation) the subjects followed the direction of eye gaze displayed by the stimulus monkeys.

Analysis revealed no bias for overall inspection time in particular quadrants. Thus we can conclude that eye gaze cues can guide attention following in the vertical or horizontal plane.

EXPERIMENT 3: HEAD AND GAZE CUES

The sequence of inspections produced at the appearance of the slide always began by a fixation on the monkey's position for Steve. Terry was also more likely to begin a trial by a fixation on monkey than on elsewhere position ("Head = Gaze": 10 M/2 E; "Head \neq Gaze": 7 M/5 E). The fixations in the elsewhere sectors were always of shorter duration than fixations on the monkey (mean number of frames, "Head = Gaze": 8.5 M, 4.5 E; "Head \neq Gaze": 6.1 M, 3.6 E) and were always followed by a fixation on the monkey position. The "first" fixation of the target or distracter positions followed the initial fixation of the monkey on 17/23 trials for Terry and 11/24 trials for Steve.

For "Head = Gaze" stimuli with the head and gaze pointing left or right, the two monkeys made more inspections of the target than of the distracter position (Figure 7a). This difference was not significant when each subject's data were analysed separately (Terry: 27/45, $p = 0.12$; Steve: 30/49, $p = 0.08$), but the target position was inspected more frequently than expected by chance when the results from both monkeys are combined (57/94, $p < 0.02$). Analysis of the "first" fixation of the target and distracter positions failed to reveal a difference between target and distracter positions when data were analysed separately by subject (Terry: 6/11, $p = 0.5$; Steve: 8/12, $p = 0.19$) or combined (14/23, $p = 0.11$).

For "Head \neq Gaze" stimuli where the face was presented in half profile with the eyes looking back at the camera, analysis of the number of inspections (Figure 7b) revealed that neither subject inspected the target more than the distracter position (Terry: 17/34, $p = 0.57$; Steve: 22/36, $p = 0.12$; combined 39/70, $p = 0.15$). Analysis of the "first" fixation of the target and distracter positions failed to reveal differential fixation of the target and the distracter positions (Terry: 6/12, $p = 0.61$; Steve: 9/12, $p = 0.07$; combined 15/24, $p = 0.08$).

The number of inspections and their duration were analysed for both subjects by a three-way ANOVA (subjects, eye/head compatibility and positions as main factors) of both inspection number and duration showed a significant main effect of position: $F(3, 3) = 37.15$, $p < 0.01$; $F(3, 3) = 14.53$, $p < 0.03$, respectively. A post-hoc analysis showed that inspection duration was increased for the target position compared to the distracter position ($p < 0.05$). There was a significant interaction of eye/head compatibility and position for number of inspections, $F(3, 3) = 17.80$, $p = 0.02$. The difference between the number of inspections made of target and distracter positions was greater for stimuli with eyes averted than with eye contact. More inspections were made in the "Elsewhere" category for stimuli with eye contact than eyes averted. This interaction between position and eye/head compatibility was also significant for inspection duration, $F(3, 3) = 10.02$, $p < 0.05$. Post-hoc analysis replicated the greater difference between target and distracter positions for the eyes averted stimuli. For both inspection number and duration, there was no main effect of subjects, $F(1, 44) = 0.85$, $p = 0.36$; $F(1, 44) = 0.04$, $p = 0.84$, or head/eye compatibility, $F(1, 1) = 49.17$, $p = 0.09$; $F(1, 1) = 3.78$, $p = 0.30$, and other interactions were non-significant (subjects and head/eye compatibility: $F(1,$

44) = 0.02, $p = 0.88$; $F(1, 44) = 0.35$, $p = 0.56$; subjects and position: $F(3, 132) = 1.07$, $p = 0.36$; $F(3, 132) = 1.03$, $p = 0.38$; subjects, head/eye compatibility, and position: $F(3, 132) = 0.14$, $p = 0.93$; $F(3, 132) = 0.16$, $p = 0.92$).

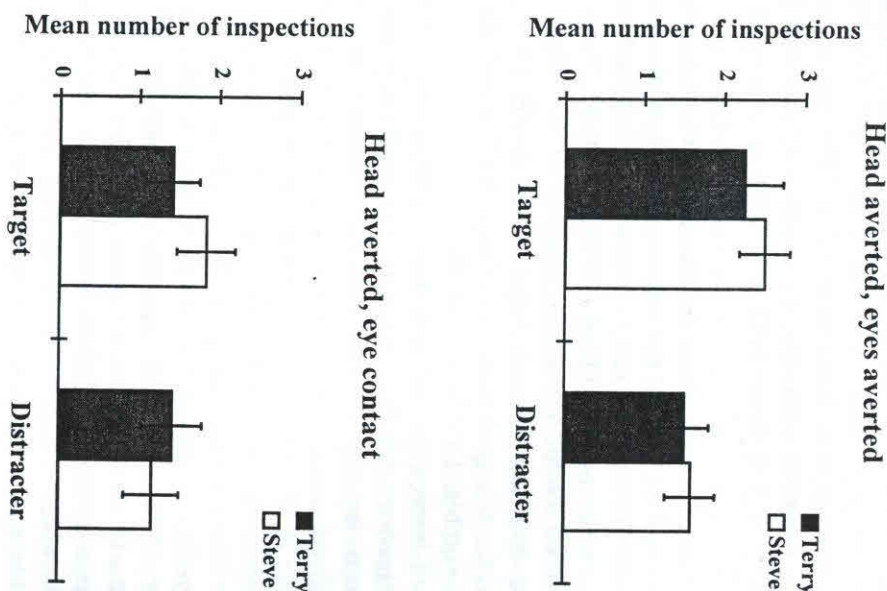


Figure 7. Number of inspections for the head and gaze stimuli. Mean number of inspections (\pm SEM) per trial made of the target and distracter positions for "Head = Gaze" stimuli with head and gaze directed laterally (upper) and for "Head \neq Gaze" stimuli with head directed laterally and gaze at the observer (lower). Each bar represents the average number of inspections over 12 trials for Terry (grey) or Steve (white).

Discussion

Experiment 3 utilised stimuli with head turned to the left or right and the eyes oriented in the same direction or looking back at the camera and observer. Attention following was predicted for stimuli with both the head and gaze oriented compatibly and directed laterally. As predicted, the ANOVA of inspection duration and inspection frequency indicated that these stimuli did provoke attention following.

For stimuli with the head turned laterally but eyes directed at the observer, we predicted less attention following than for stimuli with both eyes and head directed laterally. Stimuli with eye contact should fail to elicit pronounced attention following to lateral positions for the following reason. If the gaze is the most important index of attention direction, then the stimulus monkey can be considered to be attending in the direction of the observer, and therefore there is no reason for the observer to look to a lateral position. The observer may simply maintain attention on the face. In line with the prediction above, this bias towards the target position was significantly less marked with the eye contact stimuli than with stimuli where the gaze was turned laterally.

In summary, Experiment 3 demonstrates that monkeys show a stronger tendency to follow attention when both the head and gaze are directed to same position than when they are directed to different positions. This confirms the findings of Experiments 1 and 2: both head and gaze cues contribute to attention following.

GENERAL DISCUSSION

Static vs. dynamic stimuli

Studies of attention following that employ live stimuli invariably include movement as a cue for the attention direction. In our previous study we used dynamic video sequences of other conspecific monkeys (Emery et al., 1997). With these realistic and complex stimuli, there was clear evidence of attention following for rhesus monkeys (Emery et al., 1997). The present study confirms and extends this result by defining the visual cues that are and are not essential for attention following behaviour. The present work shows that dynamic cues are not necessary to elicit attention following in macaques. Each of the three experiments

reported here demonstrates that the two monkey subjects are behaviourally responsive to static 2-D pictorial images of other monkeys. The subjects' spontaneous reaction to the images shown was to direct their own gaze (and attention) to match the direction of attention of the monkey in the 2-D image. Static postural information is thus sufficient to drive attention following, and while eye, head, and body movements accompany the orienting behaviour of one monkey, these dynamic cues are not necessary to trigger orienting responses in an observing monkey.

Object of attention

In our current study there was no object of attention: the stimulus monkey was depicted with gaze and/or head oriented in one direction but there was no object located in this direction. Attention following in this experiment (and in the initial phase of our previous experiment, Emery et al., 1997) occurs despite the absence of an object. This lack of an object of attention contrasts with most other studies of attention following (e.g., Itakura & Tanaka, 1998). The mechanisms required to follow the direction of attention of another may be simpler than the mechanisms required to follow attention to the object of another's attention, i.e., joint attention (Emery et al., 1997).

Attention following to a spatial position is a sensible strategy because the object of another's attention may not always be visible: it may be occluded from the observer's sight (e.g. a predator hidden from the observer's line of sight). Alternatively, the focus of attention may be ambiguous because there are several candidate objects coincident with the direction of attention of the other individual. In these cases attention following to a rough spatial area can be adaptive because it can lead to the observer being more ready to react to the particular object of the other's interest, for example as soon as it moves into sight.

Cues for attention following

Experiment 1 showed that attention following is influenced by head direction but not body orientation. Experiment 2 showed that eye gaze cues alone could trigger attention following. Experiment 3 confirmed that head and gaze direction influences attention following.

Physiological studies of visual processing by macaque monkeys indicate that body orientation and posture can form a visual cue to the direction of attention or intentions of others (Perrett et al., 1992; Wachsmuth et al., 1994; Jellema et al., 1999). The current study failed to find evidence that body posture influences attention following in macaque monkeys. There are other situations in which the role of the body might be more apparent. For example, when the body posture is clearly visible but the head is occluded from sight or the head direction is ambiguous. The use of stimuli depicting these situations could provide behavioural evidence that the body can act as a visual cue to direction attention.

We have revealed a partial hierarchy in the importance of cues to attention direction. Visual cues from head posture are more important than cues from body posture. The data from Experiment 3 are consistent with the gaze being more important than the head, since changing the gaze direction with constant head direction reduced the tendency for the subjects to follow the head direction. Such data are also consistent with the head and gaze making independent contributions to the control of attention following. To obtain more definitive results on the relative importance of head and gaze, it would be more appropriate to use stimuli where the head and gaze point in different directions and neither are oriented towards the observer. We can conclude from the current experiment that attention following is controlled by both the head and gaze cues and that these are more important than body cues.

Picture perception and social behaviour

As predicted by previous studies, photographic presentations elicit interest of the monkey subjects. Indeed, both subjects were most likely to look initially at the monkey's position at the appearance of the slide, although the tone previously associated with centrally presented stimuli may have biased the subjects' initial inspections to the central area of the projection screen. Subjects also exhibited, at the beginning of the experiment, facial expressions such as lipsmacking at the sight of the monkey stimulus. The lack of behavioural response to the photographic stimuli, particularly in the eye contact configuration (Experiment 3), may simply reflect the loss of behavioural relevance from stimulus repetition. Such a habituation process when the behavioural reinforcement is absent has been reported previously, even from an early age (Sackett,

1966; Rosenfeld & Van Hoesen, 1979). The fact that emotional responses did not persist for a long period might indicate, however, that subjects perceived the stimuli as pictures rather than real conspecifics, although it remains questionable whether monkeys have knowledge of the representational nature of the picture. Nevertheless, the use of pictures provided a valid substrate for this study, as monkey subjects were able to follow attention displayed by the monkey stimulus. Care was taken to avoid habituation by the infrequent use of test stimuli and the inclusion of other control stimuli.

Attention following has been suggested to be a non-cognitive process where body cues are associated with a quasi-orienting reflex. If so, such a reflex should not need the contextual richness of a social environment (Povinelli & Eddy, 1996; Moore & Corkum, 1994; Langton & Bruce, 1999). In support of this idea, Friesen and Kingstone (1998) show that human subjects are faster at detecting a target when they have been previously primed with a simple line drawing face looking in the direction where the target will appear. Sensitivity to face patterns is also observable in newborn humans using a line drawing face (Goren et al., 1975; Johnson et al., 1991), and infants of 4 months old begin to discriminate eyes contact from gaze averted (Vecera & Johnson, 1995). Despite such sensitivity to the eye region, it is only at 18-24 months old that human infants will co-orient to another individual's gaze regardless of the format (realistic, 2D/3D) of the face or the familiarity of the cue giver (Butterworth & Jarrett, 1991; Anderson & Doherty, 1997; Corkum & Moore, 1998; Lee et al., 1998). Moreover, the faculty to determine reliably and accurately gaze direction from photographs is even not fully achieved at 4 years old in humans (Anderson & Doherty, 1997). Some forms of gaze processing, e.g., identifying whether another individual is making eye contact or not, and attention shifting may be reflexive (innate), as such capacities do not depend upon the richness and the realism of the representation. By contrast, attention following processes, which require the emission of a learned motor response (co-orientation), appear to rely upon multiple developmental factors and the fidelity of the representation (occurring minimally for schematic displays). Interpreting social information, such as attention direction, from a picture may require a greater degree of complexity in the visual and conceptual processing compared to detecting eye contact. Detailed understanding of others (e.g., comprehending desires and intentions) may depend even more on contextual information and social interaction with the other.

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RÉSUMÉ

Il est maintenant bien établi que les grands singes suivent le regard d'un humain. En dépit des évidences physiologiques rapportant la présence de cellules sensibles à la direction du regard dans le cortex temporal du macaque, peu de preuves comportementales ressortent en faveur de l'existence de capacités similaires chez les singes. Le but de cette étude a été d'étudier, à un niveau comportemental, la capacité des singes à utiliser des indices statiques provenant du regard, du visage et du corps de congénères, pour interpréter la direction de l'attention d'autrui. Nous avons enregistré le comportement visuel produit par 2 macaques rhesus à la présentation de photos de congénères dirigeant leur attention vers un endroit de l'espace. L'utilisation de photos de singes dont visage et corps étaient orientés, soit dans la même direction soit dans des directions opposées, a permis de montrer que les sujets utilisaient l'orientation du visage mais pas celle du corps pour orienter leur propre attention. Avec des photos de singes dont le visage était orienté vers l'appareil photo alors que le regard était dirigé vers la gauche, la droite, le haut ou le bas, nous avons démontré que les singes étaient capables de suivre spontanément le regard de congénères. Avec des photos de singes dont le visage était orienté à 45 degrés à gauche ou à droite, le suivi de l'attention était plus prononcé quand la direction du regard était concordante avec celle du visage que lorsque les yeux étaient dirigés vers l'observateur. Nos études démontrent que l'orientation du visage aussi bien que celle du regard influencent les réponses d'orientation de l'observateur.

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